

Skeletal Growth Histories of *Protothaca staminea* (Conrad) and *Protothaca grata* (Say) Throughout Their Geographic Ranges, Northeastern Pacific

by

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Abstract. The skeletal growth histories of only a few bivalve species have been documented throughout most or all of their latitudinal ranges. This paper considers growth parameters based on new growth measurements made throughout the geographic ranges of two bivalve species, *Protothaca staminea* (Conrad) and *P. grata* (Say). Growth data for a third species, *Siliqua patula* (Dixon, 1788) by Weymouth *et al.* are employed extensively in the study for comparative purposes. The collective range of all three species extends from the Gulf of Alaska to Panama. The parameters studied include: shell height vs. age (H_t), the rate of decrease in growth rate with ontogeny (defined as the slope of Walford plots and as e^{-k} in the von Bertalanffy growth equation), mean maximum height (H_a), and mean maximum longevity of individuals. Latitudinal trends in the number of daily growth increments formed during the first full season of growth are contrasted for individuals of both *Protothaca* species.

All three species exhibit similar growth history trends throughout their respective ranges. Northern individuals grow slowly but at more uniform rates averaged over ontogeny, and live longer than do southern phenotypes. High initial growth rates correspond to more rapid decreases in annual growth rate. The rate of growth deceleration is highly correlated with mean annual sea-surface temperatures. The number of daily growth increments formed during the first full season of growth is apparently related to the planetary gradient in sunlight and productivity. The latitudinal rate of change in the number of daily growth increments is not affected across species boundaries.

INTRODUCTION

Only a few studies have considered skeletal growth patterns over large segments of the latitudinal ranges of molluscan species (*e.g.*, WEYMOUTH *et al.*, 1931; NEWELL, 1964; ANSELL, 1968; GILBERT, 1973; BEUKEMA & MEEHAN, 1985), but attempts have not been made to relate skeletal growth aspects to latitudinal gradients in major oceanographic factors. Reduced growth rates among higher latitude phenotypes are expected based on thermodynamic arguments and the effects of pronounced seasonality in trophic resource supply. This paper presents evidence that the effects of temperature and seasonality can be at least partially distinguished based on analyses of specific skeletal growth parameters, and that the analysis of skeletal growth trends can be useful in reconstructing the life histories of fossil individuals and the states of past oceans.

The research presented is based on growth-history de-

terminations made by the author for two northeastern Pacific, intertidal, infaunal bivalves, *Protothaca staminea* (Conrad) at thirteen localities, and *P. grata* (Say) at six localities, throughout most of their composite geographic ranges from Prince William Sound, Alaska, to Panama Bay. The growth history of a third congener, *P. asperima* (Sowerby), from a single locality in Panama Bay is included. Also included are growth histories of six Pleistocene sample populations of *P. staminea* representing collections ranging geographically from Bay Center, Washington, to central Baja California, and a single collection of *P. staminea* from the Middle to Late Pliocene Etchegoin Formation of central California. Growth data provided in WEYMOUTH *et al.* (1931) based on their study of latitudinal trends in the growth of *Siliqua patula* (Dixon, 1788) are included in the analysis for comparative purposes. Geographic trends in growth-history parameters

documented for *Protothaca* include annual shell height (H_t), the rate at which growth rate decelerates with ontogeny (defined as the slope of Walford plots of growth curves and as e^{-k} of the VON BERTALANFFY [1938] growth equation), maximum mean size (H_a), and maximum mean longevity. Also included are daily growth-increment data which suggest that their number during the first full season of growth is closely tied to the planetary gradient in available sunlight and productivity, and as such may be of value in the determination of paleolatitudes, and(or) long-term trends in seasonality at specific latitudes. In all, the growth histories of more than 500 specimens of *Protothaca* are included in the analysis, approximately one-half of these from the Recent and one-half from the Pleistocene.

Protothaca staminea is the widest ranging and most intensively studied of the congeners (FRASER & SMITH, 1928; QUAYLE, 1943; SCHMIDT & WARME, 1969; FEDER & PAUL, 1973; PAUL & FEDER, 1973; PAUL *et al.*, 1976; NICKERSON, 1977; FEDER *et al.*, 1979; see also PETERSON, 1977). The species ranges from Prince William Sound, Alaska, to the southernmost tip of the Baja California peninsula, but does not occur in the Gulf of California north of La Paz. *Protothaca grata*, one of several tropical to subtropical congeners, ranges from the Pacific coast of central Baja California where its range overlaps with *P. staminea*, through the Gulf of California and as far south as Peru. In the region of overlap, both species bear striking similarities in size, shape, coloration, and surface texture. As will be shown, growth histories of both congeners within their zone of overlap are sufficiently distinct to separate the species from one another. The third species, *P. asperima*, ranges from the Gulf of California to Peru but does not overlap with *P. staminea*. It is easily distinguished from the other species of this study by its rasplike, fine surface texture, but is otherwise closer to *P. grata* in shell characteristics.

MEASUREMENT AND SAMPLING PROCEDURES

Shell heights were measured to the nearest 0.1 mm at annuli along a curved line from the umbo to the ventral margin (Figure 1). Specimens were obtained from the University of California, Los Angeles (UCLA) Department of Earth and Space Sciences Museum, the Los Angeles County Museum of Natural History (LACMNH) sections of malacology and invertebrate paleontology, and the University of California, Berkeley Museum of Paleontology (UCMP). Efforts were made to locate specimen lots that were large and composed of relatively well-preserved specimens representative of all size classes. After a series of preliminary growth-rate determinations were made, it was determined that large sample sizes were not necessary to generate representative growth curves for all localities, and several small lots (less than 10 individuals) were interposed with larger (25 or more specimens) collections. Collections of fossil specimens were selected fol-

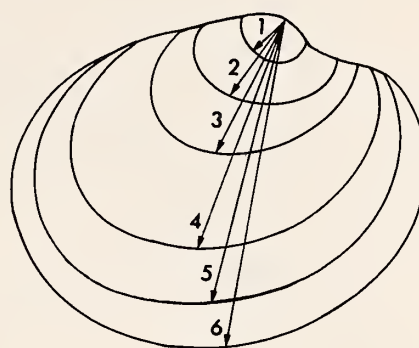


Figure 1

Measurement of shell heights at the intersections of annuli with a curved line from the umbo to the ventral margin.

lowing the same criteria as for the Recent. An additional criterion was the availability of precise stratigraphic data, particularly in relation to isotopic stage determinations (see SHACKLETON & OPDYKE, 1976; KENNEDY, 1978).

The preservation of Pleistocene shell material is generally adequate for the purpose of determining rates of annual growth. However, the quality of many Pliocene specimens was too poor to permit accurate direct determinations of growth break positions. In some cases this problem was overcome by plotting specimens on a Walford plot (SHELDON, 1965, and see below). In other cases, annuli weathered out as resistant ridges on the surface of otherwise poorly preserved specimens, undoubtedly an artifact of the denser packing of growth increments during the slow-growth season, and this provided useful data.

SOURCES OF GROWTH-ANNULUS VARIATION

Several sources of variation in mean annual height vs. age data can be identified: sample size, the number of individuals surviving to a specific age, geographic dispersion in the length of the spawning season (and therefore, in conditions experienced when juvenile growth is initiated), carry-over effects of earlier growth increases into later growth stages, and the latitudinal gradient in the length of the growing season. Standard deviations in data compiled for *Protothaca staminea* throughout its range (HARRINGTON, 1986) indicate that sample size is not a major factor in the variability of height vs. age. Because survivorship falls with increasing age, the number of individual data points determining a given age class's mean size declines, but normally this does not affect the smoothness of the growth curve until less than about five specimens represent a given age class. Standard deviations in height vs. age data do not measurably increase in *Protothaca* with ontogeny.

Geographic differences in the duration of the spawning season and dispersion in the time of settlement have a more dramatic effect on latitudinal trends in the variance of size

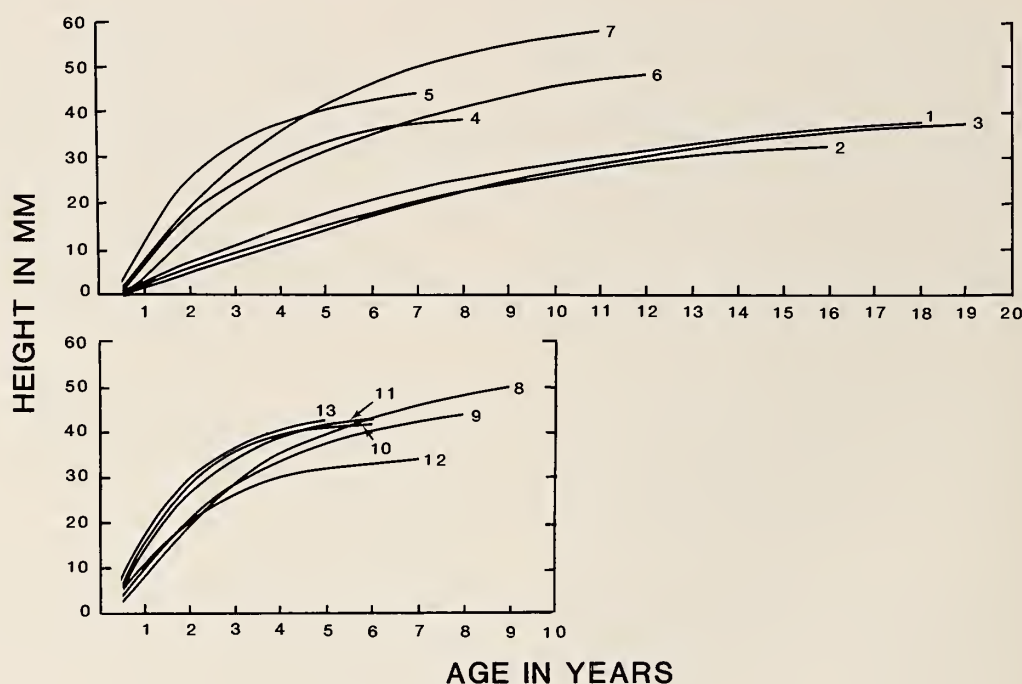


Figure 2

Shell height vs. age curves of 13 Recent collections of *Protothaca staminea* throughout its range. 1, Whittier, AK; 2, Kayak Is., AK; 3, Dall Is., AK; 4, 5, Puget Sound, WA; 6, coastal Oregon; 7, Humbolt, CA; 8, Cayucos, CA; 9, Morro Bay, CA; 10, Long Beach, CA; 11-13, Baja California, Mexico: 11, Estero Punta Banda; 12, Rosarita Bay; 13, Santa Maria Bay. Note the general increase in the convexity of curves and reduced longevity progressing from northern to southern localities.

vs. age data. At high latitudes, spawning in *Protothaca staminea* is limited to the month of June and standard deviations in size vs. age data are exceptionally small (FEDER *et al.*, 1979; and see NICKERSON, 1977). At lower latitudes near Victoria, B.C., however, spawning takes place from April to October (QUAYLE, 1943) and standard deviations there are substantially greater. KINNE (1972) has noted progressive increases in the duration of the spawning season for many temperate invertebrates with decreasing latitude. CRAIG (1967) observed more scatter in the position of growth rings in bivalve species sampled at Bimini lagoon when compared to higher latitude (temperate) species and suggested that this may reflect more continuous recruitment throughout the year in the Bimini species. Hence, where spawning is spread throughout more of the year greater standard deviations in shell heights are predicted among individuals of a given age.

GROWTH HISTORIES

Growth curves of Recent *Protothaca* specimens are summarized in Figures 2 and 3. Table 1 contains a listing of Walford slopes for *Protothaca* and *Siliqua patula* throughout the study region as a function of sea-surface temperature. Walford plots were constructed for each sample in order to estimate the rate of growth deceleration, maximum

mean size, and maximum longevity of average individuals (WALFORD, 1946; HANCOCK, 1965; SHELDON, 1965, CERRATO, 1980) (Figure 4). Because of the asymptotic approach of growth curves to a horizontal line, maximum shell heights must be estimated when employing Walford plots. In this study, maximum height is taken where 98% of H_{t+1} (shell height at time t plus one year) has been obtained by H_t . The age that corresponds to this shell height is taken as the mean maximum longevity of individuals from the habitat.

Latitudinal Trends in Growth Histories

At the northern range end points of all three species studied the rate of growth is slower, growth rate deceleration is less pronounced (see below), and longevity is greater than at their southern range end points. Maximum sizes of *Protothaca staminea* are not observed at extreme high latitudes, but somewhat south (Table 1). This reflects almost negligible height increases during the first few years of growth for this species in the Gulf of Alaska. In *P. grata* and *Siliqua patula*, initial growth rates are not as markedly reduced at their northern range end points and the maximum sizes are obtained there.

Walford plot slopes represent a quantification of the rate at which growth decelerates with ontogeny equivalent

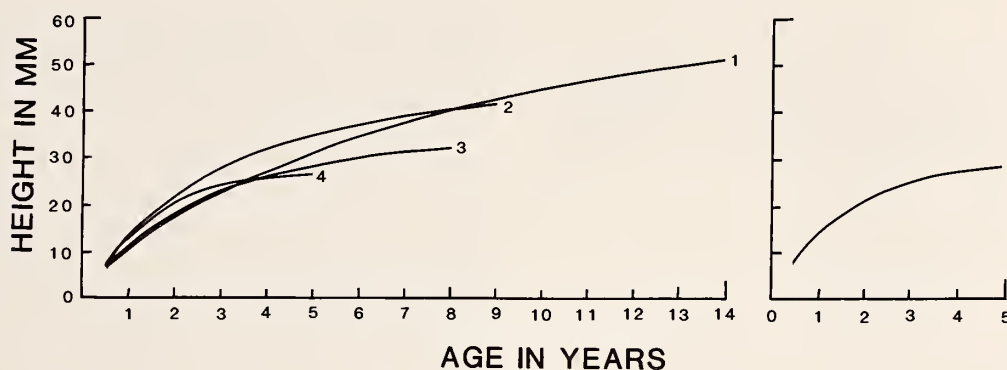


Figure 3

Representative shell height vs. age curves of *Protothaca grata* (1-4), and *P. asperrima* (5). 1, Cholla Bay, head of the Gulf of California; 2, Magdalena Bay, Mexico; 3, Mazatlan, Mexico; 4, Panama Bay; 5, Panama.

to e^{-k} in VON BERTALANFFY'S (1938) growth equation. High Walford slopes represent relatively steady growth increases from year to year while progressively lower slopes reflect increasingly pronounced convexity in size vs. age curves. For *Protothaca*, slopes decrease from north to south beginning with a value of 0.91 for *P. staminea* from Prince William Sound, Alaska, decreasing to a minimum value of 0.49 for a sample from Santa Maria Bay (central Baja California). *Protothaca grata* specimens also exhibit a maximum Walford slope (0.89) at the taxon's northern range end point at the head of the Gulf of California, and a minimum value (0.55) near the southern range end point of the species at Panama Bay. A Walford plot for the species *P. asperrima* from a single locality at Venado Island in the Canal Zone (near that taxon's southern range end point) was constructed yielding a slope of 0.52. Thus, in the northern hemisphere, Walford slopes on the order of 0.90 typify post-inflection growth of northern range end-point individuals of *Protothaca*, while values of 0.50 (or slightly less) typify the growth of individuals near southern range end points.

Slopes for *Siliqua patula* range from a maximum of about 0.70 at the northern range end point in the Gulf of Alaska, and gradually decrease to a minimum of about 0.33 at the southern range end point near Pismo, California. Although these end-point values are less than those of *Protothaca*, it is interesting to note that the range of values is approximately the same (roughly 0.40). The reasons for this discrepancy in range end-point values are not understood. It is possible that the differences arise from the significantly more compressed shell geometry of *Siliqua*.

Walford slope values for *Protothaca staminea*, *P. grata*, and *Siliqua patula* are plotted against mean annual sea-surface temperature estimates taken for each region by interpolating between 0.5°C surface isotherms determined for the northeastern Pacific by ROBINSON & BAUER (1976) (Figure 5). A slightly higher temperature (i.e., 8.6°C vs. 7.5°C) was taken for Prince William Sound, Alaska, representing April through September mean monthly tem-

peratures only (NICKERSON, 1977). This step was taken so that the temperature estimate was approximately in line with that actually experienced by *Protothaca* during its growth season in the region. Excellent correlations were obtained with $r = -0.938$ for *P. staminea*, $r = -0.842$ for *P. grata*, and $r = -0.935$ for *S. patula*, suggesting that mean annual temperature is a principal environmental factor determining the slope of the Walford plot, and hence the rate of annual growth deceleration.

Two samples from Puget Sound yielded seemingly anomalous slopes of 0.68 and 0.62. As a check for consistency, data from Fraser and Smith (1928) for *Protothaca staminea* at Victoria, B.C., yield a value of 0.70. However, K. Cheu at the University of Washington Department of Ecology (personal communication, 1985) advises that mean temperatures within the sound are easily 4°C warmer on many of the tidal flats than along the Washington outer coast. This indicates mean annual temperatures for Puget Sound tidal flats are approximately 12.5°C. Hence, Walford slopes close to those observed at Cayucos and Morro Bay, California (e.g., 0.74 and 0.69, respectively) (Table 1) should in fact be expected for the Puget Sound area.

A second latitudinal anomaly in Walford slopes occurs along northern Baja California, Mexico, where they are higher than expected for the latitude. As indicated on ocean-surface temperature maps (ROBINSON & BAUER, 1976), however, the northern Baja California region is a site of pronounced coastal upwelling, and mean surface temperatures there are nearly identical to the more northern Long Beach, California locality (Table 1). South of these areas of upwelling, the decreasing trend in Walford slopes with latitude may be resumed; the southernmost sample of *Protothaca staminea* from central Baja California possesses a Walford slope (0.49) slightly lower than any of the other collections. Here temperatures are substantially warmer, averaging about 17.5°C.

As previously noted, the southernmost range of *Protothaca staminea* overlaps along the central and southernmost outer coast of southern Baja California with the north-

Table 1

Walford slopes (e^{-k}), mean annual sea-surface temperatures, and geographic locations of samples. Temperatures from ROBINSON & BAUER (1976) except for Alaskan localities of *Protothaca staminea*, which are from NICKERSON (1977).

Species	Walford slope (e^{-k})	Water temperature °C	Location
<i>Protothaca staminea</i>	0.91	8.6	Whittier, AK
<i>Protothaca staminea</i>	0.87	8.6	Kayak Island, AK
<i>Protothaca staminea</i>	0.90	8.6	Dall Island, AK
<i>Protothaca staminea</i>	0.68	12.5	Puget Sound, WA
<i>Protothaca staminea</i>	0.62	12.5	Puget Sound, WA
<i>Protothaca staminea</i>	0.83	11.8	Oregon
<i>Protothaca staminea</i>	0.78	12.2	Humbolt, CA
<i>Protothaca staminea</i>	0.74	13.5	Cayucos, CA
<i>Protothaca staminea</i>	0.69	13.5	Moore Bay, CA
<i>Protothaca staminea</i>	0.51	16.0	Long Beach, CA
<i>Protothaca staminea</i>	0.59	14.5	Punta Banda, Mex.
<i>Protothaca staminea</i>	0.59	14.5	Rosarita Bay, Mex.
<i>Protothaca staminea</i>	0.49	17.5	S. Maria Bay, Mex.
<i>Protothaca grata</i>	0.89	21.5	Cholla Bay, Mex.
<i>Protothaca grata</i>	0.68	23.0	Guaymas, Mex.
<i>Protothaca grata</i>	0.74	22.0	Magdalena Bay, Mex.
<i>Protothaca grata</i>	0.69	25.5	Mazatlan, Mex.
<i>Protothaca grata</i>	0.63	27.5	Nicaragua
<i>Protothaca grata</i>	0.55	27.3	Panama
<i>Siliqua patula</i>	0.68	6.8	Hallo Bay, AK
<i>Siliqua patula</i>	0.69	6.8	Swickshak, AK
<i>Siliqua patula</i>	0.71	7.2	Karls Bar, AK
<i>Siliqua patula</i>	0.64	9.2	Masset, AK
<i>Siliqua patula</i>	0.48	11.5	Copalis, WA
<i>Siliqua patula</i>	0.54	12.2	Crescent City, CA
<i>Siliqua patula</i>	0.33	13.5	Pismo, CA

ernmost range of *P. grata*, and the taxonomic separation of the two species based on gross morphological grounds is difficult within their zone of range overlap. Growth histories are useful in distinguishing these species, however. Two collections from the Magdalena Bay region exhibit markedly different Walford slopes of 0.49 and 0.74 for *P. staminea* and *P. grata*, respectively.

PALEOTEMPERATURE DETERMINATIONS

Growth-history curves are presented for six Pleistocene and a single Pliocene collection in Figure 6. Slopes were used to infer paleotemperatures (from Figure 5) and these were compared with paleotemperature determinations based on isotopic stage data (see SHACKLETON & OPDYKE, 1976; KENNEDY *et al.*, 1982) (Figure 7) and the distribution of cold and warm temperature molluscan faunas (KENNEDY, 1978, 1979; KENNEDY *et al.*, 1979, 1982; EMERSON *et al.*, 1981) for the Pleistocene of the Pacific coast. In general,

paleotemperature estimates based on the regression of Walford slopes with modern sea temperatures are in good agreement with data provided from the sources cited above. The following discussion is organized from the youngest to the oldest specimen localities.

One of the youngest samples (LACMNH loc. 6913) is from the 40,000–60,000 year-old, mid-Wisconsin terrace at Isla Vista (Goleta) near Santa Barbara, California. The age would place the collection in isotopic stage 3 of SHACKLETON & OPDYKE (1976), a period of very cold water even at this comparatively low latitude. The Walford slope obtained for this sample is 0.84, indicative of a mean annual temperature on the order of 10.3°C, about 4°C colder than the mean for this section of the coast today. KENNEDY (1978) has noted that the faunas at this locality and along the Santa Barbara and Ventura coastlines contain several cold-water species presently restricted to the Columbian Molluscan Province.

Cold water is implied by the growth histories of two specimens from Cape Blanco, Oregon (UCMP A-8712) that are of approximately the same age as the cold-water Isla Vista collection (above). KENNEDY (1978) has noted a number of species with modern-day Aleutian affinities at Cape Blanco. Walford slopes suggest slightly colder paleotemperatures compared to those of Isla Vista. For Cape Blanco a slope of 0.87 was determined suggesting a mean annual temperature of about 9.6°C. Although the slope is based on only two specimens, both exhibited nearly identical skeletal growth histories.

Two localities, UCLA loc. 4722 from Santa Cruz, California, and LACMNH loc. 5662 from Bay Center, Washington, have been assigned by KENNEDY (1978) to isotopic stage 5a (SHACKLETON & OPDYKE, 1976), a time of cooler conditions than occur today. According to Kennedy, Columbian temperatures may have persisted at least as far south as central California (*e.g.*, not as far south as during the colder isotopic stage 3, above); however, the faunal compositions at Santa Cruz indicate water temperatures somewhat warmer than expected when compared to the fauna at Point Año Nuevo only a few miles north. Kennedy has attributed this to the coastal physiography of Monterey Bay, and the lack of upwelling there. J. F. Wehmler (unpublished, *in* KENNEDY, 1978) notes anomalous warm air temperatures for the latitude at Santa Cruz occurring today. The Walford slope for the Santa Cruz collection indeed reflects warmer than expected paleotemperatures given the climatic framework of isotopic stage 5a. The computed slope of 0.60 would suggest an approximate mean annual paleotemperature of 14.5°C. Based on very limited data for the Bay Center region, Kennedy suggests paleotemperatures very close to modern temperatures. The paleotemperature suggested in the Walford plot of the Bay Center specimens supports this interpretation; a slope of 0.86 suggests a paleotemperature of about 9.8°C.

Two other Pleistocene localities are approximately 120,000 years old, a time of unusually warm temperatures (isotopic stage 5e). The first (UCLA loc. 2314) is from

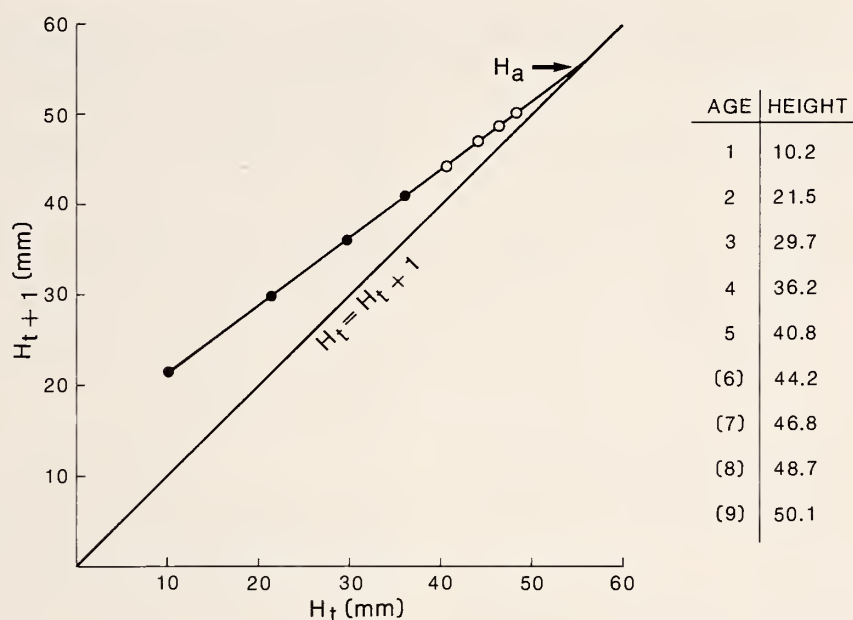


Figure 4

Construction of a Walford plot from height vs. age data (right). The horizontal axis represents shell height (mm) at a given age (years). The vertical axis represents shell height one year later. Open circles are values derived from the growth equation ($H_{t+1} = b + mH_t$), where m is the slope of the Walford plot and b is the intercept with the vertical axis. H_a describes the intersection of the Walford plot line with a line of no growth where $H_t = H_{t+1}$.

the Palos Verdes Sand, type locality of the Pleistocene Verdean Province. Specimens yield a Walford slope of 0.58, indicative of temperatures approaching 15°C. The second (a composite of UCLA locs. 3447 and 3445) was taken slightly to the north at the type locality of the Pleistocene Cayucan Province, and indicates a paleotemperature of about 11.2°C based on a Walford slope of 0.79. The large temperature change over this relatively short geographic distance during isotopic stage 5e is not surprising. The collections are separated by a major physiographic transition centering today on Point Conception, and this results in the clustering of sea-surface isotherms there. If the paleotemperature estimates above are correct, they suggest the currently steep latitudinal thermal gradient was maintained between the Verdean and Cayucan Provinces during isotopic stage 5e.

The single Pliocene collection (UCLA loc. 3491) is from the Etchegoin Formation of Kern County, California. For these probable Middle to Late Pliocene age specimens, growth under relatively cool-water conditions is expected (ADDICOTT, 1970). A Walford slope of 0.65 was determined for a sample of 30 specimens, suggesting a mean annual temperature of about 13.5°C.

Despite the unknowns concerning the precision of temperature values projected from Walford plots, and the first-order approximations of temperature based on maps of sea-surface isotherms, the use of Walford slopes as an estimate of paleotemperatures appears promising. The ob-

vious next step in the research should be to determine Walford slopes based on a large number of Recent species throughout their geographic ranges, especially from locations where mean annual temperatures have been previously determined. A second future line of research should be to contrast Walford temperature estimates with determinations based on isotopic compositions of shell material.

LATITUDINAL TRENDS IN DAILY GROWTH-INCREMENT NUMBERS

Criteria employed in the recognition of daily growth increments for *Protothaca* follow KENNISH (1980) for *Mercentaria mercenaria* and other references cited in RHOADS & LUTZ (1980). Latitudinal trends in daily growth-increment data (Figure 8) are based on observations in thin-section, acetate peels, and in polished shells embedded in resin blocks. The determination of the number of increments formed within the first growing season is important because numbers decline with ontogeny. Preliminary evidence suggests that the rate of this decline also varies with latitude (Figure 9). In some specimens small areas of the umbonal region were abraded and the number of increments had to be estimated. This was done by measuring the distance across the abraded area and then dividing by the average thickness of adjacent increments. This procedure should have introduced an error of no greater than about 10 increments.

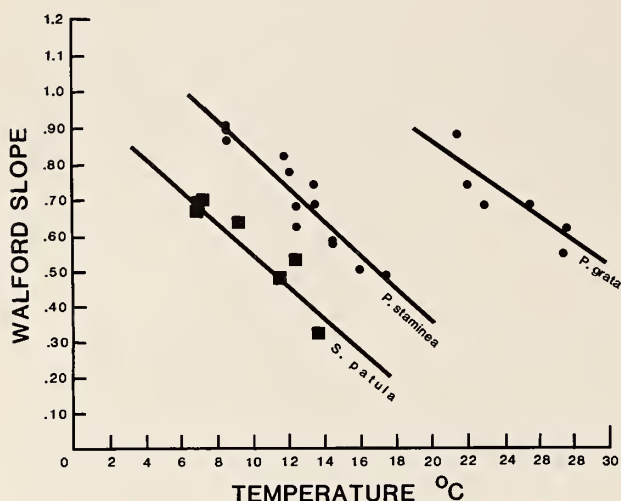


Figure 5

Walford slopes plotted against mean annual sea-surface temperature (see text) for *Protothaca staminea*, *P. grata*, and *Siliqua patula* samples collectively ranging from the Gulf of Alaska to Panama.

The maximum number of daily increments formed during the first full growing season increases systematically with decreasing latitude (Figure 8), and the trend is not interrupted where congeners overlap. In the Gulf of Alaska, the maximum number of daily growth increments is about 150, suggesting that *Protothaca staminea* is metabolically growth-active for only about five months out of each year. Progressing southward, the numbers of increments increase gradually such that at Panama Bay, they number about 331.

The latitudinal trend in increment numbers parallels the global seasonal pattern of primary productivity in the world's oceans (CUSHING, 1959a, b; MENZEL & RYTHER, 1960; RYTHER & MENZEL, 1960; RAYMONT, 1963). A

regular trend in the duration and amplitude of primary productivity undoubtedly affects the length of the growing season. At high latitudes the season is short and peaked. Progressing toward the equator, the amplitude of the productivity curve flattens substantially, often consists of two modes at mid-latitudes, and very near the equator is extremely low, but of much greater duration. The global distribution of available sunlight is considered of principal importance in the initiation of annual productivity, whereas the role of temperature is relatively minor. This being the case, then it should be expected that the regular trend in daily increment numbers vs. latitude (Figure 8) should more closely reflect trophic resource seasonality patterns than temperature effects.

DISCUSSION

Several factors structure the growth histories of post-larval individuals throughout the northeastern Pacific range of *Protothaca*. Two of the most important factors are the range of temperatures experienced by individuals, and the seasonal pattern of primary productivity. Other factors such as salinity and water chemistry are considered to contribute a relatively insignificant effect on growth-history differences over the broad geographic scale evaluated in the study.

Temperature is known to determine the rate at which food may be metabolized, and hence, should substantially affect the seasonal pattern of increasing and decreasing daily increment thicknesses. Such trends have been well documented for a number of bivalve taxa (*e.g.*, PANNELLA & MACCLINTOCK, 1968; RHOADS & PANNELLA, 1970; ARTHUR *et al.*, 1983). The effect of seasonal patterns in trophic resource abundance on the thicknesses of daily growth increments, and questions involving the energetics of calcium carbonate precipitation over the range of temperatures that bivalve species experience, remain as important areas of future research.

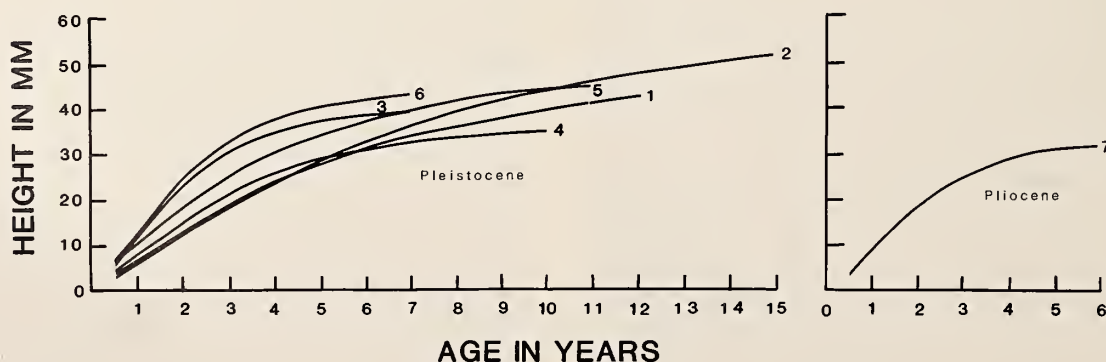


Figure 6

Pleistocene (1-6) and Pliocene (7) shell height vs. age curves of *Protothaca staminea*. 1, Isla Vista, CA; 2, Cape Blanco, OR; 3, Santa Cruz, CA; 4, Bay Center, WA; 5, Palos Verdes, CA; 6, Cayucos, CA; 7, Etchegoin Fm., central CA.

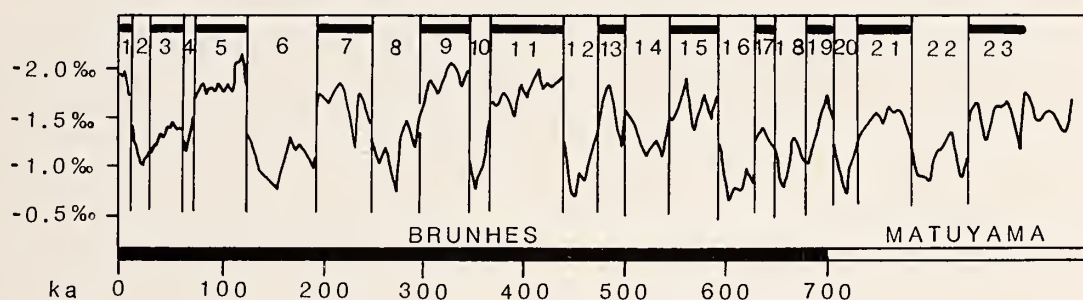


Figure 7

Isotopic stages redrawn from SHACKLETON & OPDYKE (1976). Peaks represent relatively warmer paleotemperatures.

The seasonal pattern of trophic resource supply is clearly important in determining the length of the growing season at different latitudes and this is apparently best recorded in the number of growth increments formed during the first full season of growth experienced by individuals. However, as shown earlier (Figure 9) the number of increments recorded within annual growth bands decreases systematically with increasing age. One explanation for this decline could be that ever-increasing energy is expended each year in other metabolic activities such as reproduction and maintenance. It has yet to be determined, however, if fewer days are recorded at the beginning of the growth season, at the end, or if the pattern of growth increment formation is simply more intermittent throughout the year. This hypothesis could be tested by contrasting some measure of the seasonal pattern of reproductive effort against growth expenditures for a series of age classes.

Near the southern range end point of a species, the growing season is relatively longer, and temperatures warmer on the average, than along more northern segments of its range. The combination of these factors acts to maximize the initial annual growth rate of *Protothaca*. Whether the higher rate of growth deceleration and reduced longevity at lower latitudes are consequences of initial (perhaps wasteful) growth expenditures as has been suggested by WEYMOUTH *et al.* (1931), or whether they result from the relaxation of selection for continued size increases after a minimum adaptive size is obtained, is unclear. Transplantation experiments (*e.g.*, SEED, 1968) that document rejuvenated growth late in life argue against models based on pre-determined lifetime metabolic allocations.

One explanation arises if the relatively reduced rate of ontogenetic growth deceleration (and increased longevity) is viewed from the standpoint of potential lifetime reproductive commitments. For example, if high latitude phenotypes followed a similar schedule of growth rate decline as their low latitude counterparts, their size and potential reproductive contributions at any given age would be volumetrically reduced (Harrington, in preparation). Hence, high-latitude individuals may rely on a strategy that acts, perhaps through allelic substitutions, to maximize the duration of growth activity each season, and perhaps to in-

crease longevity. Table 2 contrasts predicted total lifetime reproductive contributions for individuals near the range end points and range midpoint of *Protothaca staminea*, assuming that fecundity is uniformly a 50% function of soft-tissue volume. Although this tabulation represents only gross estimates of lifetime reproductive effort, it is significant in two respects. First, the reproductive contributions for individuals located near the respective range end points are nearly identical. This suggests that range end points may not be determined by thermal effects per se (*i.e.*, heat or cold death) but by population recruitment effects stemming from (temperature and seasonality-dependent) growth-history patterns. Secondly, individual reproductive contributions and potential population recruitment levels are maximized near the range midpoint of the species. Thus, it should be expected that population sizes are greatest and perhaps most stable there (see BROWN, 1984).

Viewed from the standpoint of relative life-history strategies (STEARNS, 1976), it is apparent that northern range end-point representatives, in effect, hedge their reproductive bets by virtue of delayed contributions (due to slower

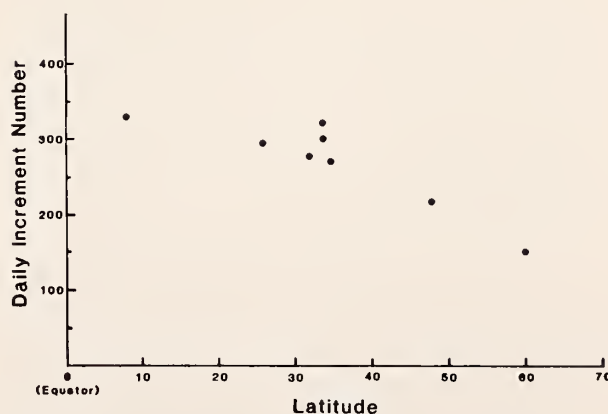


Figure 8

The number of daily growth increments formed during the first full season of growth (see text) based on single specimens of *Protothaca* from the Gulf of Alaska to Panama.

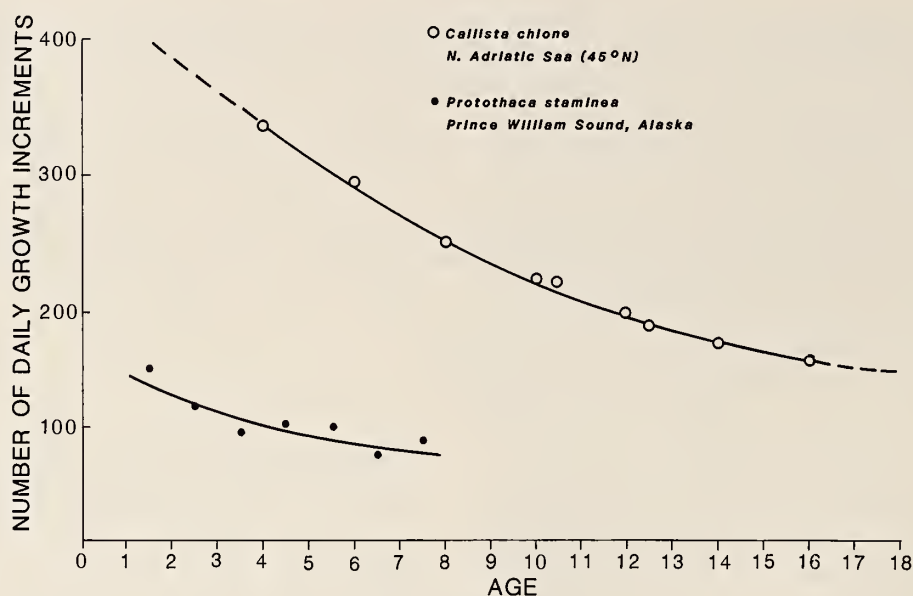


Figure 9

Ontogenetic decrease in the number of daily growth increments for a specimen of *Protothaca staminea* from the Gulf of Alaska (lower curve) and *Callista chione* (upper curve) from the northern Adriatic Sea. Data for *C. chione* are extracted from HALL (1975) by combining the number of growth increments in the "fast growth band" and the "biocheck" at given ages from Hall's curve (HALL, 1975:fig. 4). Note that the rate of decrease is greater for *C. chione*.

growth) and significantly greater longevity. Meanwhile, southern phenotypes can be viewed as relative *r*-strategists; reproductive contributions are maximized among relatively young individuals. For example, by age 4 the southern phenotypes have produced as many potential offspring per capita as do northern phenotypes by age 12 (Table 2). In terms of actual population recruitment potentials for *Protothaca staminea* this analysis awaits data based on latitudinal differences in survivorship. For *Siliqua patula*, however, the general pattern is of progressively lower age-specific mortality at higher latitudes (WEYMOUTH *et al.*, 1931). If this survivorship trend also applies to *Protothaca*, then smaller age-specific reproductive efforts among young, northern individuals should be at least partially overcome by the more significant reproductive contributions of relatively larger, older age classes.

The employment of growth-history patterns may provide useful data to a variety of paleontological problems. Potential paleotemperature applications have been suggested in a previous section. As a paleobiogeographic tool the patterns observed suggest a means by which the geographic position of a fossil sample with respect to its species range end points might be suggested. For example, Walford slopes of approximately 0.90 should indicate proximity to northern, and values of approximately 0.50 to southern range end-point positions.

Latitudinal trends in the number of daily growth increments formed during the first full season of growth may

Table 2

Estimated age-specific shell volumes for individuals of *Protothaca staminea* from northernmost, mid-range, and southernmost localities. Total reproduction is taken as one-half of the sum of shell volumes at age. Volumes derived from curve in HARRINGTON (1986).

Age (yr)	Gulf of Alaska		Cayucos, CA		Baja California	
	Height (mm)	Volume (mL)	Height (mm)	Volume (mL)	Height (mm)	Volume (mL)
1	2.69	<1.0	10.23	1.2	14.90	1.8
2	5.76	<1.0	21.54	2.7	27.10	4.3
3	8.93	1.0	29.70	6.0	34.30	9.0
4	12.63	1.5	36.20	10.5	38.53	12.8
5	15.68	1.9	40.76	16.0	41.04	16.4
6	18.20	2.3	44.13	20.0	42.51	18.2
7	20.58	2.5	46.73	24.2	—	—
8	22.82	2.9	48.66	27.8	—	—
9	24.50	3.5	50.10	30.7	—	—
10	26.10	3.9	51.18	31.5	—	—
11	27.49	4.4	51.97	33.0	—	—
12	28.71	5.1	—	—	—	—
13	29.78	6.0	—	—	—	—
14	30.70	6.5	—	—	—	—
15	31.51	7.0	—	—	—	—
16	32.22	7.5	—	—	—	—
Total volume		58.0		175.8		62.5
Total production		29.0		87.9		31.2

provide information useful in documenting latitudinal translations of crustal blocks. Because high-latitude phenotypes should typically record a low number of increments, shells from high-latitude fossil deposits bearing anomalously high increment numbers in the first annulus should signal that large-scale latitudinal translations may have occurred. However, much more data are needed in order to determine the generality of the association between increment numbers and latitude. In addition, increment numbers may be useful in the evaluation of finer-scale trends in seasonality over given latitudinal regions.

As a potential tool in the correlation of rock units, growth-history analysis may lead to more precise local correlations reflecting localized temperature effects. Refined stratigraphic subdivisions of fossiliferous rock units may be based on at least three growth-history criteria: (1) the rate of growth deceleration, (2) initial annual growth rates, and (3) the thickness of growth increments and their rate of decline in numbers during ontogeny.

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LITERATURE CITED

- ADDICOTT, W. C. 1970. Latitudinal gradients in the Tertiary molluscan faunas of the Pacific coast. *Palaeogeog., Palaeoclimatol., Palaeoecol.* 8:287-312.
- ANSELL, A. D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographic range. *Jour. Cons. Perm. Int. Explor. Mer* 31:364-409.
- ARTHUR, M. A., D. F. WILLIAMS & D. S. JONES. 1983. Seasonal temperature-salinity changes and thermocline development in the mid-Atlantic Bight as recorded by the isotopic composition of bivalves. *Geology* 11:655-659.
- BEUKEMA, J. J. & B. W. MEEHAN. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar. Biol.* 90:27-34.
- BROWN, J. H. 1984. On the relationship between abundance and distribution of species. *Amer. Natur.* 124:255-279.
- CERRATO, R. M. 1980. Demographic analysis of bivalve populations. Pp. 417-465. *In:* D. C. Rhoads & R. H. Lutz (eds.), *Skeletal growth of aquatic organisms*. Plenum: New York.
- CRAIG, G. Y. 1967. Size-frequency distributions of living and dead pelecypods from Bimini, Bahamas, B.W.I. *Jour. Geol.* 75:34-45.
- CUSHING, D. H. 1959a. On the nature of production in the sea. *Fish. Invest. Lond. Series II.* 22:1-40.
- CUSHING, D. H. 1959b. The seasonal variation in oceanic productivity as a problem in population dynamics. *Jour. Cons. Perm. Int. Explor. Mer* 24:455-464.
- EMERSON, W. K., G. L. KENNEDY, J. F. WEHMILLER & E. KEENNAN. 1981. Age relations and zoogeographic implications of Late Pleistocene marine invertebrate faunas from Turtle Bay, Baja California Sur, Mexico. *Nautilus* 95:105-116.
- FEDER, H. M. & A. J. PAUL. 1973. Abundance estimates and growth rate comparisons for the clam *Protothaca staminea* from three beaches in Prince William Sound, Alaska with additional comments on size-weight relationships, harvesting and marketing. *Univ. Alaska Inst. Mar. Sci. Tech. Report No. R73-3:34* pp.
- FEDER, H. M., J. C. HENDEE, P. HOLMES, G. J. MUELLER & A. J. PAUL. 1979. Examination of a reproductive cycle of *Protothaca staminea* using histology, wet-dry weight ratios, and condition indices. *Veliger* 22:182-187.
- FRASER, C. M. & G. M. SMITH. 1928. Notes on the ecology of the littleneck clam, *Paphia staminea* Conrad. *Trans. Roy. Soc. Can. Ser. 3, 22, Sect. V:*249-269.
- GILBERT, M. A. 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). *Biol. Bull.* 145:119-126.
- HALL, C. A., JR. 1975. Latitudinal variation in shell growth patterns in bivalve molluscs: implications and problems. Pp. 163-175. *In:* G. D. Rosenberg & S. K. Runcorn (eds.), *Growth rhythms and the history of the earth's rotation*. John Wiley and Sons: London.
- HANCOCK, D. A. 1965. Graphical estimation of growth parameters. *Jour. Cons. Perm. Int. Explor. Mer.* 29:340-351.
- HARRINGTON, R. J. 1986. Growth patterns within the genus *Protothaca* (Bivalvia: Veneridae) from the Gulf of Alaska to Panama: paleotemperatures, paleobiogeography, and paleolatitudes. Doctoral Thesis, University of California, Santa Barbara. 235 pp.
- KENNEDY, G. L. 1978. Pleistocene paleoecology, zoogeography and geochronology of marine invertebrate faunas of the Pacific Northwest coast (San Francisco Bay to Puget Sound). Doctoral Thesis, University of California, Davis. 824 pp.
- KENNEDY, G. L. 1979. Pleistocene marine faunal provinces of California. Appendix to K. R. LaJoie, J. P. Kern, J. F. Wehmiller, S. A. Mathieson, A. M. Sarna-Wojcicki, R. F. Yerkes & P. A. McCrory (1979), *Quaternary marine shorelines and crustal deformation, San Diego to Santa Barbara, California*. Pp. 3-15. *In:* P. L. Abbott (ed.), *Geological excursions in the southern California area* (Dept. Geol. Sci., San Diego State Univ., San Diego).
- KENNEDY, G. L., K. R. LAJOIE & J. F. WEHMILLER. 1979. Late Pleistocene and Holocene zoogeography, Pacific northwest coast. *Geol. Soc. Amer. Abstr. Prog.* 11:87.
- KENNEDY, G. L., K. R. LAJOIE & J. F. WEHMILLER. 1982. Aminostratigraphy and faunal correlations of late Quaternary marine terraces, Pacific coast, USA. *Nature* 299:545-547.
- KENNISH, M. J. 1980. Shell microgrowth analysis: *Mercenaria mercenaria* as a type example for research in population dynamics. Pp. 255-294. *In:* D. C. Rhoads & R. A. Lutz (eds.), *Skeletal growth of aquatic organisms*. Plenum: New York.

- KINNE, O. 1972. Temperature. Pp. 321-616. In: O. Kinne (ed.), Marine ecology Vol. 1. Wiley Interscience: London.
- MENZEL, D. W. & J. H. RYTHER. 1960. The annual cycle of primary production in the Sargasso Sea, Bermuda. Deep Sea Res. 6:351-367.
- NEWELL, N. D. 1964. Physiological aspects of the ecology on intertidal molluscs. Pp. 59-81. In: R. M. Wilbur & C. M. Yonge (eds.), Physiology of Mollusca. Vol. 1. Academic Press: London.
- NICKERSON, R. B. 1977. A study of the littleneck clam (*Protothaca staminea* Conrad) and the butter clam (*Saxidomus giganteus* Deshayes) in a habitat permitting coexistence, Prince William Sound, Alaska. Proc. Natl. Shellfish Assoc. 67:85-102.
- PANNELLA, G. 1975. Paleontological clocks and the history of the earth's rotation. Pp. 253-284. In: G. D. Rosenberg & S. K. Runcorn (eds.), Growth rhythms and the history of the earth's rotation. John Wiley and Sons: London.
- PANNELLA, G. & MACCLINTOCK. 1968. Biological and environmental rhythms reflected in molluscan shell growth. Jour. Paleontol. 42:64-80.
- PAUL, A. J. & H. M. FEDER. 1973. Growth recruitment and distribution of the littleneck clam, *Protothaca staminea* in Galena Bay, Prince William Sound, Alaska. Fish Bull. 7: 665-677.
- PAUL, A. J., J. M. PAUL & H. M. FEDER. 1976. Recruitment and growth in the bivalve *Protothaca staminea* at Olson Bay, Prince William Sound ten years after the 1964 earthquake. Veliger 18:385-392.
- PETERSON, C. H. 1977. Competitive organization of the soft-bottom macrobenthic communities of southern California lagoons. Mar. Biol. 43:343-359.
- QUAYLE, P. B. 1943. Sex, gonad development and seasonal gonad changes in *Paphia staminea* (Conrad). Jour. Fish. Res. Bd. Canada 6:140-151.
- RAYMONT, J. E. G. 1963. Plankton and Productivity in the Oceans. Pergamon Press: New York. 660 pp.
- RHOADS, D. C. & R. H. LUTZ (eds.). 1980. Skeletal growth of aquatic organisms. Plenum: New York. 750 pp.
- RHOADS, D. C. & G. PANNELLA. 1970. The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3:143-161.
- ROBINSON, M. K. & R. A. BAUER. 1976. Atlas of North Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. Naval Oceanographic Office, Washington, D.C.
- RYTHER, J. H. & D. W. MENZEL. 1960. The seasonal and geographic range of primary production in the Western Sargasso Sea. Deep Sea Res. 6:235-238.
- SCHMIDT, R. R. & J. E. WARME. 1969. Population characteristics of *Protothaca staminea* (Conrad) from Mugu Lagoon. Veliger 12:193-199.
- SEED, R. 1968. Factors influencing shell shape in *Mytilus edulis* L. Jour. Mar. Biol. Assoc. U.K. 48:561-584.
- SHACKLETON, N. J. & N. D. OPDYKE. 1976. Oxygen isotope and paleomagnetic stratigraphy of Pacific core V28-239, late Miocene to latest Pleistocene. Geol. Soc. Amer. Mem. 145: 449-464.
- SHELDON, R. W. 1965. Fossil communities with multi-modal size-frequency distributions. Nature 206:1336-1338.
- STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.
- VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws II). Human Biol. 10:181-213.
- WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90:141-147.
- WEYMOUTH, F. W., J. C. McMILLIN & W. H. RICH. 1931. Latitude and relative growth in the razor clam *Siliqua patula*. Jour. Exp. Biol. 8:228-249.